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WITHIN-SEASON DIFFERENCES IN GROWTH OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*

CYNTHIA JONES¹

ABSTRACT

Data obtained from two previous studies of larval Atlantic herring growth were compared, based on otolith increment estimated age. These data, from the Gulf of Maine in 1976-77 and 1978-79, supported the hypothesis that larvae hatched early in the spawning season grew faster than larvae hatched late. Differences were significant under assumptions that increments were deposited in the otolith either daily or at 0.5 increments per day. Corroborative evidence indicated that otolith increments were formed daily at least during the early part of the spawning season.

The otolith increment technique has been used to estimate age and growth in field-caught larval Atlantic herring, *Clupea harengus harengus*, in the Gulf of Maine by Townsend and Graham (1981) and by Lough et al. (1982). Use of the increment technique to estimate age usually assumes daily deposition of otolith increments. Uncertainty exists, however, regarding increment deposition rates in the otoliths of larval herring. Gjosaeter (1981) and Øiestad (1982) have observed daily increment deposition. In contrast, Geffen (1982) found that increment deposition can be variable and a function of growth rate in larval herring, underscoring the problem in simply assuming that increments occur daily under field conditions. Growth calculations based on assumptions of daily increment deposition in populations that experience variable increment deposition rate would result in inaccurate estimates of growth rates. In most cases where otolith increment deposition has been tested under suboptimal conditions, the deposition rate has been found to be nondaily (for review see Jones 1984). Estimates of growth rates can be made, however, by expressing growth based on increment counts and with the use of corroborative evidence to determine periodicity of increment deposition.

Das (1968) found that growth rates of larval Atlantic herring, measured by following the progression of length modes over time, were different within a spawning season. He stated that early-spawned larvae grew faster than late-spawned larvae and modeled growth with curvilinear functions. Townsend and Graham (1981) also reported two different growth

rates for Atlantic herring, one for larvae born prior to November 5 and one for larvae born later. Each group was modeled by two regression lines to emphasize that growth ceased in January and resumed in February. In their study, early- and late-hatched groups were analyzed separately and the comparison of growth between larvae hatched early versus late in the season was not statistically verified.

This paper uses otolith increment data from Townsend and Graham (1981) and from Lough et al. (1982) to compare early-season versus late-season larval Atlantic herring growth. The comparisons are made using the assumptions of both daily and nondaily otolith increment deposition.

METHODS

Raw data for otolith counts and larval fish lengths used in these studies were obtained from Gregory Lough of the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA, and from Joseph Graham and David Townsend of the Maine Department of Marine Resources, Boothbay Harbor, ME. Both data sets were used in the detection of within-season differences in growth rates. Although the study of Lough et al. (1982) encompassed a larger area, only data from the Gulf of Maine were included in the analysis (Table 1), in order that comparisons were made within the same area as for Townsend and Graham (1981). Methods employed for the collection of data were reported by Lough et al. (1982) and by Lough and Bolz (1979) for the 1976-77 data and by Townsend and Graham (1981) for the 1978-79 data.

For each season (1976-77, 1978-79), data were analyzed in three ways:

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TABLE 1.—Station information for Atlantic herring samples from the Gulf of Maine area for the fall and winter of 1976-77 sampling program. (Data from Lough et al. 1982.)

Vessel	Cruise No.	Stn.	Lat. N	Long. W	Date	Time (Night or Day)
<i>Annandale</i>	76-01	38	43°37'	69°22'	8 Oct.	0300 (N)
		44	43°44'	68°50'	8 Oct.	1415 (D)
		59	44°25'	67°35'	9 Oct.	1515 (D)
		65	44°36'	67°07'	13 Oct.	0330 (N)
<i>Researcher</i>	76-01	102	42°58'	70°00'	8 Dec.	1030 (N)
		105	43°30'	69°30'	9 Dec.	1100 (N)
<i>Mt. Mitchell</i>	77-01	122	43°14'	70°01'	24 Feb.	1620 (D)
		123	43°00'	70°15'	24 Feb.	1933 (D)

- 1) Hatch date was calculated on the assumption of daily increment deposition, and all data were considered.
- 2) Hatch date was calculated on the assumption of daily increment deposition only with larvae which had 60 or fewer increments included for analysis. This was done to determine whether growth differences were present in the earlier months of life. Also, since the range of increment counts for the late-hatched larvae from 1976 to 1977 was greater than for early-hatched larvae, use of a truncated data set resulted in more valid comparisons.
- 3) Hatch date was calculated on the assumption of nondaily deposition (0.5 increment/d).

Date of hatching was calculated by subtracting the estimated age of each larva from its date of capture. This calculation, of course, depends on how age was estimated. According to the Lough et al. (1982) calculation, a larva with 10 otolith increments would be 29 d old: 22 d for the first 3 increments, plus 7 d to lay down the next 7 increments. According to the assumptions used by Townsend and Graham (1981), a larva with 10 otolith increments would be 15 d old, assuming that increment deposition began 5 d after hatch, and was daily thereafter. There is a difference of 14 d between these two estimates of age, and, therefore, estimated day of hatch. This does not affect the regression analysis, as long as the independent variable used is increment count, not age.

The range of possible hatch dates for each individual was also calculated, based on the consideration that deposition rates could vary from 0.5 to 1.0 increment/d (after Geffen 1982). Age could be equal to the number of increments plus a constant (5 d) or up to twice the number of increments plus a constant (5 d).

Larvae were classified as either early- or late-hatched within the spawning season. For 1976-77

the early-late division date was placed at the discontinuity in the frequency of hatching plot, which also occurred at the midpoint in the spawning cycle. Division date for the 1978-79 data set was placed at approximately the division of Townsend and Graham (1981) which they felt represented two different groups of larvae.

For analysis of nondaily deposition, the data were partitioned to insure that there could be no overlap of early- and late-hatched classification of larvae, assuming deposition ranged from daily deposition to deposition of one increment every 2 d. Any late-hatched larva whose possible range of hatch dates overlapped the division date (for early-hatched vs. late-hatched classification) was eliminated from analysis. This resulted in a loss of data (e.g., the fish whose possible hatch date overlapped the division date) and decreased the ability to detect differences.

Ordinary least squares linear regressions were fit to each data set. Bartlett's test for homogeneity of variance (Ostle and Mensing 1975) was applied to the data before each analysis. After regressions were fit, the residuals of length were plotted against predicted length and examined for trends (Draper and Smith 1981). *F*-tests (Ostle and Mensing 1975) were applied to paired linear regressions, early-hatched versus late-hatched, to determine whether the slopes were significantly different. This test showed whether the data were better fit by two lines, one for early-hatched and one for late-hatched larvae, or whether a single regression line was preferable. In the regression plots the change in length is expressed in millimeters per increment.

The von Bertalanffy growth equation,

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)})$$

was also fitted to the data, using the nonlinear regression procedure (NLIN) within SAS (Statistical Analysis Systems, SAS Institute, Cary, NC). Estimates of the parameters (K , L_{∞} , t_0) of the von Bertalanffy equations for early- and late-hatched larvae were compared with a Fisher-Behrens test (Hoenig 1982) to determine whether the vector of parameter estimates from the two classifications was significantly different.

RESULTS

Linear regression models fitted to larval length-at-increment count data showed significant differences between larvae hatched early and late in the spawning season. Larvae hatched early had achieved greater length at a given increment count than those

hatched later. Intercepts were not compared since the data sets did not contain any larvae with fewer than seven increments and inferences outside the range of the data should not be drawn.

1976-77 Study

A frequency plot of hatching dates for the Gulf of Maine stations is shown in Figure 1 for age estimated on the assumption of daily ring deposition and

in Figure 2 for age estimated on the assumption that deposition was daily or as little as one ring every other day.

Differences in length-at-increment count between early- and late-hatched larvae was striking (Table 2). Regression plots are shown in Figure 3. Analysis of the data confirmed that the length-at-count data were modeled more accurately by two different regression lines ($P < 0.01$) and that the slopes of these two regressions were significantly different (P

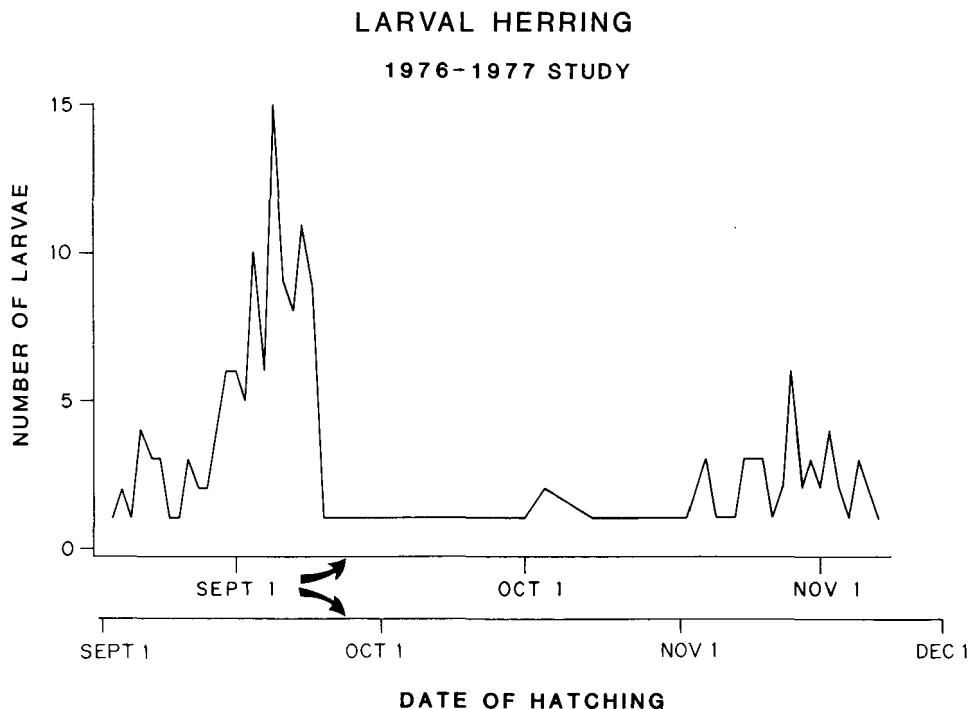


FIGURE 1.—Frequency of Atlantic herring hatching during the 1976-77 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method, or, as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

TABLE 2.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	64	15.8	0.0948	0.0047	0.87		
60 or fewer	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	44	14.6	0.1470	0.0274	0.41		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early versus late for each group.

LARVAL HERRING

1976-1977

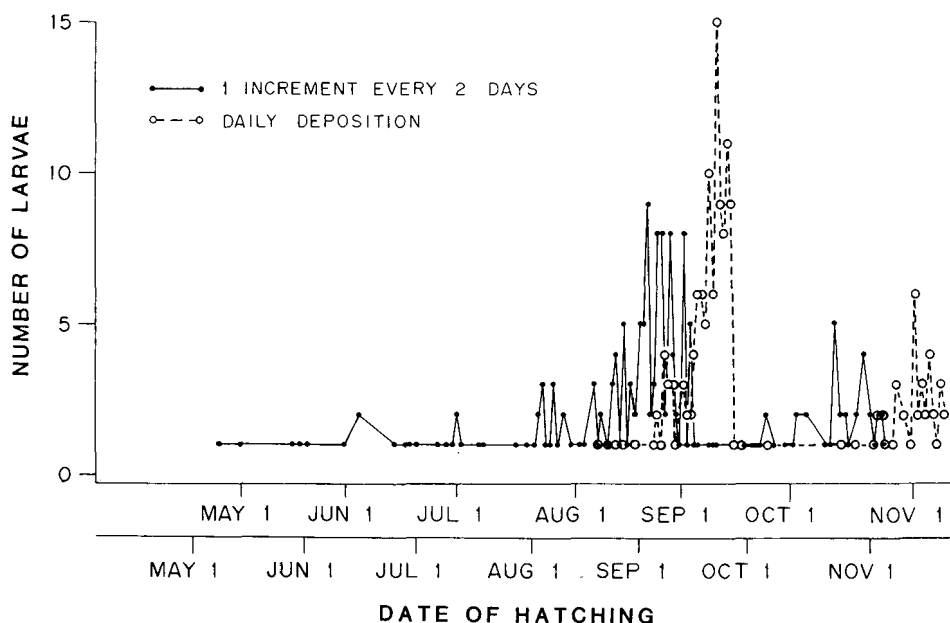


FIGURE 2.—Frequency of Atlantic herring hatching during the 1976-77 study, calculated under two assumptions of otolith increment count and age relationship.

< 0.01). The average length achieved per increment was 0.33 mm and 0.10 mm for early- and late-hatched larvae, respectively. Bartlett's test confirmed that variances were homogeneous. Analysis of residuals showed that the last three residuals, corresponding to the three largest larvae, were below the average. The exclusion of these points did not alter the results of the analysis.

Analysis of the subset of larvae with fewer than 60 increments (Table 2) showed that data were better fitted with two different regression lines ($P < 0.01$) and that the slopes were significantly different ($P < 0.01$). Regression plots are shown in Figure 4. Change in length of early-hatched larvae was 0.33 mm/increment and 0.15 mm/increment for late-hatched larvae. Bartlett's test showed variances to be homogeneous and residuals showed no trends, except for the two youngest late-hatched larvae which fell below the regression line. Late-hatched larvae were slightly larger than early-hatched larvae for the lowest increment counts.

Differences in length-at-increment count were apparent for data whose calculated hatch dates included deposition rates of from 0.5 to 1.0 increments/d (Table 3). The change in length of early-

hatched larvae was 0.33 mm/increment compared with 0.17 mm/increment for late-hatched larvae. Data were again better fit with two regression lines ($P < 0.01$) whose slopes were significantly different ($P < 0.01$).

The von Bertalanffy growth equation fit the late-hatch larval data well (Table 4). L_{∞} was estimated at 29.81 mm, with a 95% confidence interval of 26.41 to 33.22 mm. Fit to the early-hatched larval data was poor. L_{∞} was estimated at 35.59 mm, with a confidence interval of 17.76 to 53.41 mm. These data were adequately fit with a straight line, and there is little justification for fitting with a curvilinear function other than it has been traditionally used for adult fish. Beverton and Holt (1954), however, stated that the von Bertalanffy equation should not necessarily be used during the early life stages. Nevertheless, when the parameter estimates from the two curves were compared, they were signifi-

FIGURE 4.—Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Lough et al. (1982).

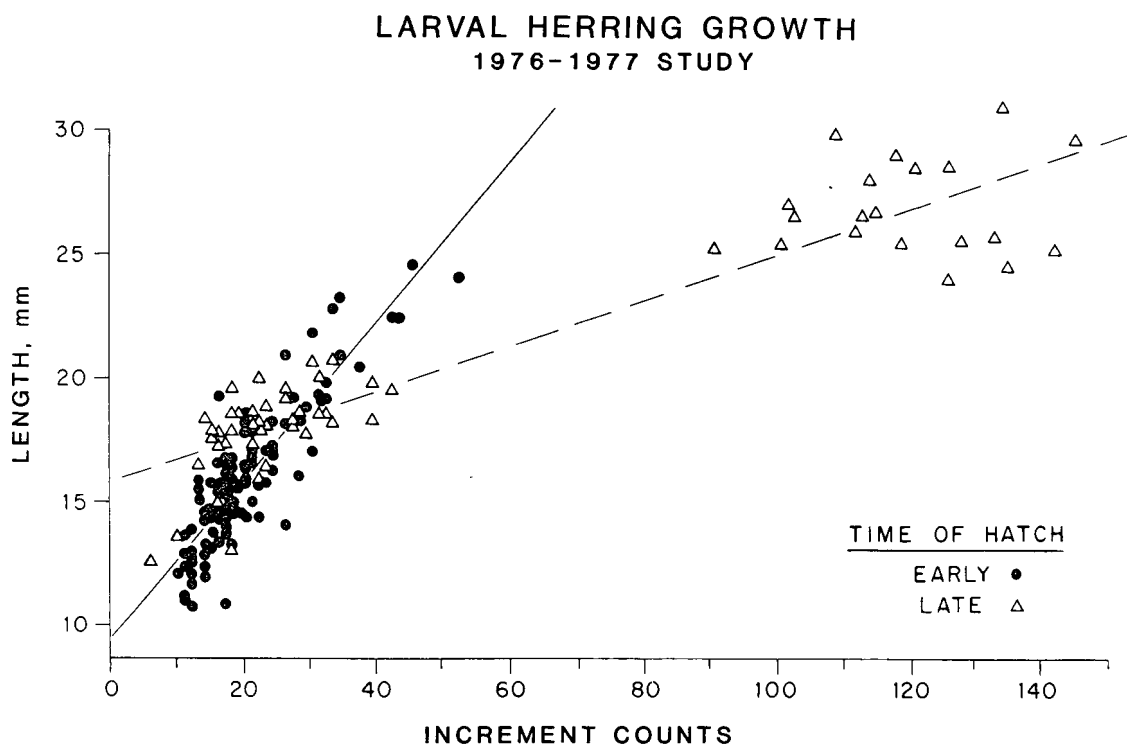


FIGURE 3. - Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Lough et al. (1982).

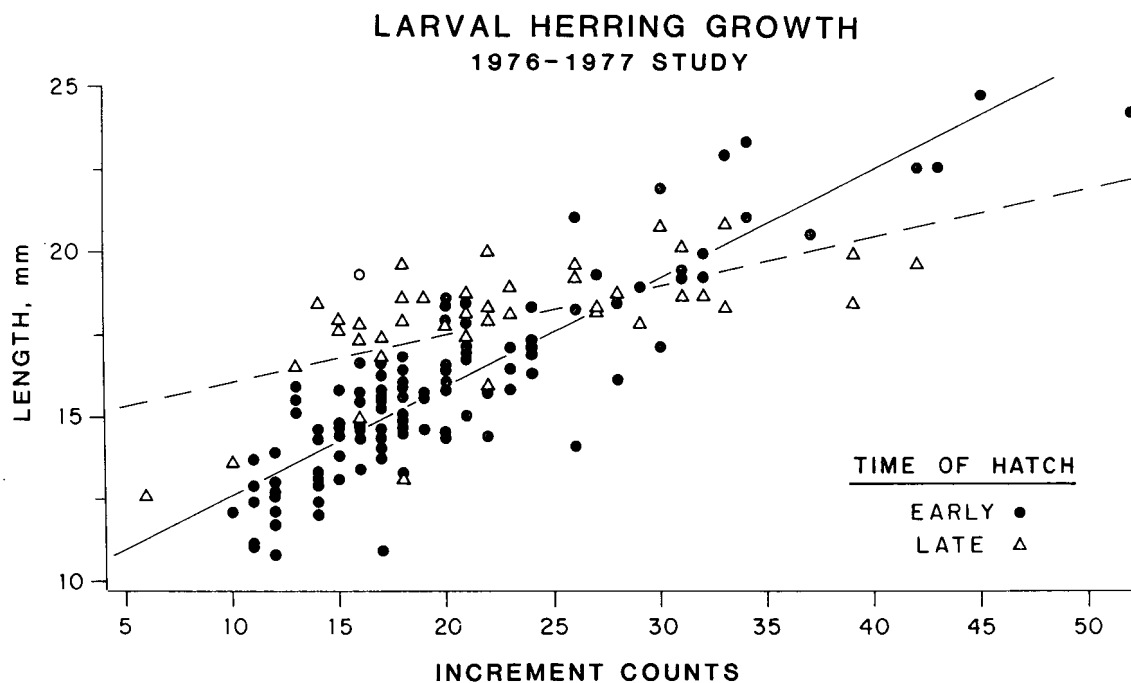


TABLE 3.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data based on two otolith increment deposition assumptions. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	39	14.2	0.1711	0.0364	0.37		

Legend: Data were classified into early- and late-hatched larvae. Two dates of hatch were calculated: 1) Age equalled increment count plus a constant, and 2) age equalled twice the increment count plus a constant. This resulted in a range of potential hatching dates. Any late-hatched larva whose range of hatch date overlapped the division date (Text Fig. 1) was eliminated from the analysis.

TABLE 4.—Estimation of von Bertalanffy growth parameters for larval Atlantic herring from the Gulf of Maine.

Year	Hatch classification	Parameter	Estimate of parameter	Standard error of estimate	95% confidence interval	
					Low	High
1976-77	Early	K	0.01865	0.00939	0.00008	0.03723
		L_{∞}	35.6	9.0	17.8	53.4
		t_0	-12.3	5.00	-22.2	-2.41
	Late	K	0.01530	0.00457	0.00616	0.02443
		L_{∞}	29.8	1.7	26.4	33.2
		t_0	-38.01	12.46	-69.92	-13.10
1978-79	Early	K	0.00262	0.00158	-0.00050	0.00575
		L_{∞}	113.2	48.8	16.3	210.1
		t_0	-42.28	9.94	-62.00	-22.57
	Late (convergence criteria could not be met)					

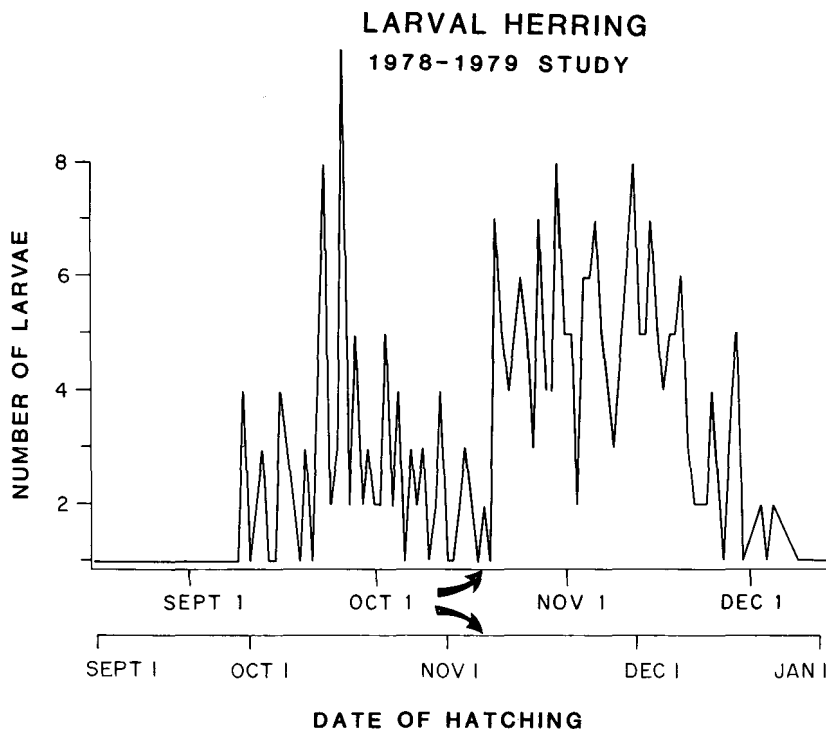


FIGURE 5.—Frequency of Atlantic herring hatching during the 1978-79 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

cantly different ($P < 0.01$)—early-hatched larvae grew faster than late-hatched larvae.

1978-79 Study

A frequency plot of hatching dates under the assumption of daily increment deposition for larvae sampled in the Sheepscot estuary is shown in Figure 5.

Analysis (Table 5) showed that the data were better fit with two lines ($P < 0.01$) and that the slopes were different ($P < 0.01$). The change in length was 0.21 mm/increment and 0.18 mm/increment

for early- and late-hatched larvae, respectively (Fig. 6). However, the results should be interpreted with the knowledge that Bartlett's test showed the variances to be heterogeneous. This could have been caused by actual heterogeneity of variances, or by nonnormality in the data. The F tests used in these analyses assumed equal variances between the hatch classifications. Cochran (1947) reported, however, that lack of homogeneity would decrease the power of an F test to discern true differences when they did, in fact, occur. Since differences were statistically significant, not meeting this assumption did not hinder analysis (the use of various transformations

TABLE 5.—Regression analysis of 1978-79 Gulf of Maine Atlantic herring data. (Data from Townsend and Graham 1981.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	102	13.3	0.2134	0.0661	0.92	<0.01	<0.01
	Late	198	14.2	0.1793	0.0060	0.82		
60 or fewer	Early	42	9.4	0.3378	0.0189	0.89	<0.01	<0.01
	Late	53	11.4	0.2434	0.0203	0.74		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early vs. late for each group.

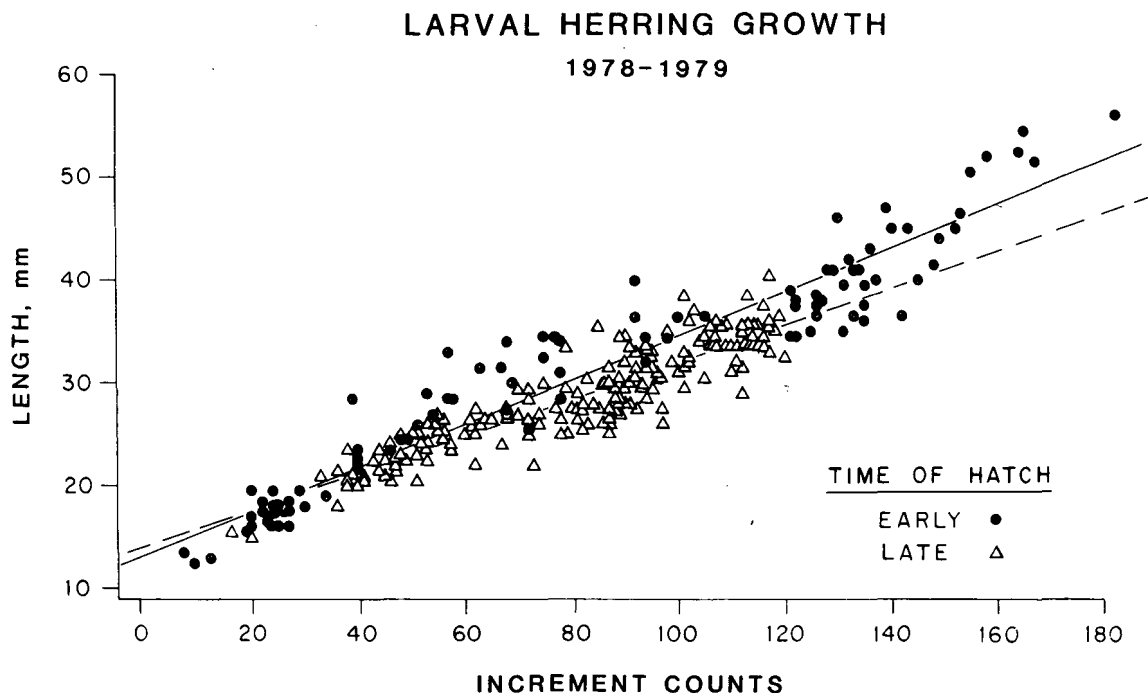


FIGURE 6.—Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Townsend and Graham (1981).

did not result in homogeneity of variances). Except for the residuals for three small larvae, analysis for residuals showed no trends.

For larvae with 60 increments and fewer (Fig. 7), Bartlett's test showed homogeneity of variance. These data were better fitted by two lines ($P < 0.01$); the slopes were significantly different ($P < 0.01$). The change in length was 0.34 mm/increment and 0.24 mm/increment for early- and late-hatched larvae, respectively.

The von Bertalanffy growth equation fit the early-hatched larval data poorly (Table 4). L_{∞} was estimated at 113.22 mm, with a 95% confidence interval of 16.37 to 210.06 mm. The von Bertalanffy growth function could not be fitted (solution would not converge) to the late-hatched larval data.

The 1978-79 data could not be tested under assumptions that increment deposition could vary from 0.5 to 1.0 increment/d. Almost all of the calculated hatch dates for late-hatched larvae, estimated on deposition rates of 0.5 increment/d, overlapped the classification division date. Too few points were left for analysis.

DISCUSSION

Evidence from the Gulf of Maine supports the

hypothesis that increase in length for herring larvae hatched early in the spawning season is greater than for larvae hatched late in the season. These differences were evident both under assumptions of daily otolith increment deposition and for deposition of one increment every other day. Before these differences are assumed to be due to differences in growth, however, there are other hypotheses which should be considered that could explain these observations. Differences could be the result of within-season changes in otolith increment deposition rates, or of differential mortality due to selective predation.

If there are within-season changes in otolith increment deposition rates, growth (change in length at age) could actually be similar, but the calculated growth rates would appear to be different because they are expressed as change in length per increment count. In order for this hypothesis to explain the above results, larvae born early in the season would be required to put down fewer increments per time period than would larvae born late in the season. The data allow a test of the hypothesis that larvae lay down fewer than 1 increment/d during the early part of the year. When estimated hatching dates are calculated for larvae caught early in the season, under the assumption that one increment was deposited every other day, some of these larvae

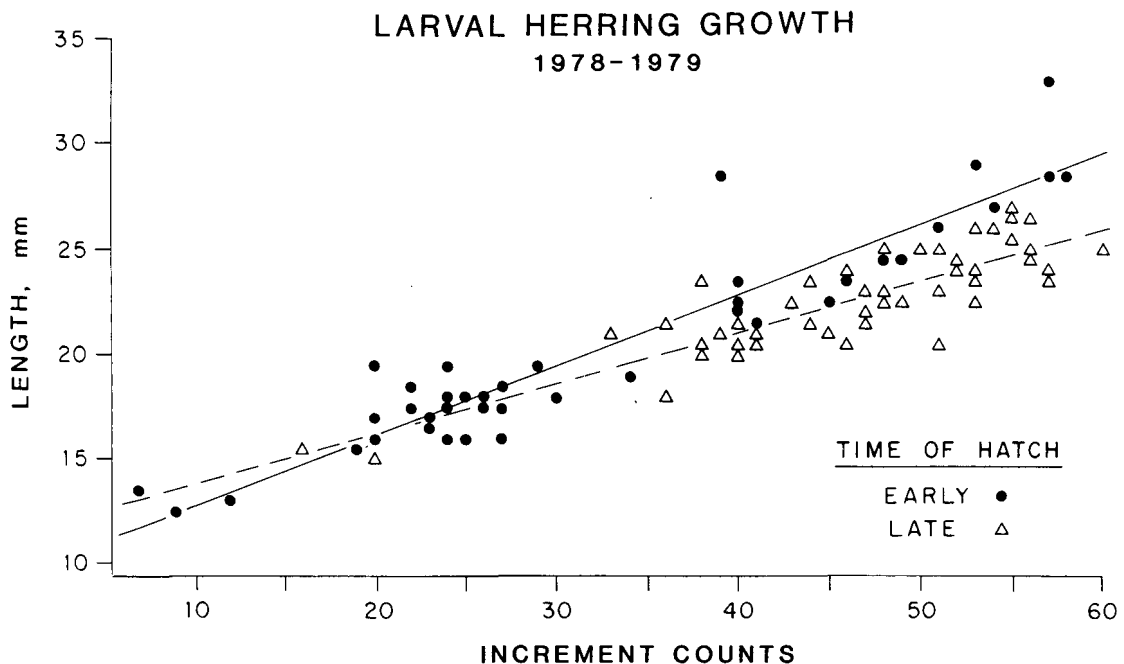


FIGURE 7. — Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Townsend and Graham (1981).

would have had to appear in the plankton in the middle of the summer (Fig. 3). However, newly hatched larvae are not found in significant numbers in the plankton before September (Boyar et al. 1973; Colton et al. 1979). It is far more plausible that larvae hatched early in the season, when growing conditions are more nearly optimal (Sherman and Honey 1971; Cohen and Lough 1983), deposit increments with close to daily periodicity. Hence, in order for this hypothesis to be true, late-hatched larvae would have to deposit increments at a rate greater than 1 increment/d. There is no evidence in the literature to support this for larval herring.

Difference in population growth rates within a spawning season could also result from a shift in size-specific mortality during the season. The observed differences in growth rate could result if early-hatched larvae have higher cumulative mortalities for slower growing individuals, while late-hatched larvae have higher mortalities for faster growing individuals. Progressively, fewer and fewer of the selectively predated larvae would be seen in older ages. This would result in differences in population growth rates that are not apparent for individuals within the population.

Although differential mortality cannot be dismissed with the available data, the most plausible explanation for the differences in length-at-increment count is an actual difference in larval growth rate over the spawning season. Such differences in population growth rate can be important for larval herring survival. Since greater time spent in the larval stage is thought to be related to increased mortality, it is interesting to note that an early-hatched larva from the 1978 study would require, on the average, 80 d to reach 30 mm, compared with 88 d for a late-hatched larva. For the 1976 study, it would take, on the average 63 d for an early-hatched larva to reach 30 mm compared with 157 d for a late-hatched larva to reach this size.

It has been shown that in both years, late-hatched larvae are larger than early-hatched larvae at the time of first increment formation. This could result from larger eggs being produced in the winter (Cushing 1967), or from different growth rates from hatch to the age of larvae covered in this study. Without further evidence of differences in egg size or actual growth rates between hatch and the age these studies began, neither hypothesis can be supported.

Differences in growth rate within the spawning season can contribute to error when using an age-length key to age larvae. For a given length, samples containing early-hatched larvae would yield different

ages than samples containing late-hatched larvae. For the 1978-79 study (under the assumption of daily increment deposition), a 25 mm larva would average 60 increments for early-hatched larvae versus 56 for late-hatched larvae. For the 1976-77 study a larva of this length would average 47 versus 102 increments, respectively. This additional variation should be taken into consideration when using age-length keys for larvae.

Differences in growth during the spawning season might be due to changes in the environment when a species of fish spawns over a protracted time period, such as Atlantic herring which spawns from late August through November (Boyar et al. 1973; Colton et al. 1979). Early in the season copepods, the main food for larval herring (Sherman and Honey 1971; Cohen and Lough 1983), are more abundant than late in the spawning season (Sherman et al. 1983). Temperatures average 12°-16°C early in the season and < 8°C later in the season (Colton 1968; Colton and Stoddard 1972). Day length and metabolic demand may also vary over the spawning season. Alternately, differences in growth between larvae hatched early and late in the season could be the result of genetic differences if early and late spawners are from different stocks.

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